
THE *PROSOECA PERINGUEYI* (DIPTERA: NEMESTRINIDAE) POLLINATION GUILD IN SOUTHERN AFRICA: LONG-TONGUED FLIES AND THEIR TUBULAR FLOWERS¹

John C. Manning² and Peter Goldblatt³

ABSTRACT

A guild of 28 winter- and spring-flowering species of two plant families, Iridaceae and Geraniaceae, with intense purple to crimson flowers and extremely long and slender perianth tubes, is pollinated exclusively by two long-tongued flies of the family Nemestrinidae. The two species of flies, *Prosoeca peringueyi* and *P. sp. nov.*, are active in the late winter and spring, have large bodies, mouthparts 20–50 mm long, and forage for nectar while hovering. Plants pollinated by these two flies share a suite of convergent floral characteristics, including a straight or slightly curved floral tube at least 20 mm and up to 70 mm long, relatively short petals or tepals colored predominantly dark blue- or red-purple with pale nectar guides, and anthers and stigmas exerted from the tube and usually unilateral in orientation. With one exception, the flowers of all species secrete large amounts of nectar of relatively constant total sugar concentration, mostly 24–29%, and high sucrose:hexose ratio. Most members of the guild have odorless flowers. The long floral tube makes nectar unavailable to most insects, including a variety of bees, wasps, and other flies that pollinate plants which co-occur with members of the long-tubed flower guild. The two *Prosoeca* species have mouthparts long enough to forage effectively on these long-tubed flowers, and they are also effective pollinators because pollen adheres to their bodies and is transported from flower to flower. The flies visit a wide range of plants but are effective pollinators only of those with tube lengths greater than their proboscis lengths. We have identified four mutually exclusive sites of pollen deposition on the insects' bodies: when two or more members of the guild co-occur, each species typically utilizes a different pollen deposition site. This suggests that pollen contamination is detrimental to reproductive success. Differential pollen deposition sites may have evolved in response to selection for reduced pollen contamination. Since 27 of the 28 plant species appear to depend exclusively on these two species of *Prosoeca* for pollination, these flies must be considered keystone species in the ecosystems where they occur.

A close association between the form and color of flowers and pollination by a particular pollinator is well known. Convergence in floral morphology among species that rely on the same pollinator class led to the recognition of floral syndromes (Faegri & van der Pijl, 1979; Grant, 1981; Vogel, 1954). Those species with morphologically similar flowers that share the same pollinator species constitute a particular pollination guild, an extension of the term (Root, 1967) describing a group of species that exploits the same class of resources in a similar way. A guild is thus a functional unit independent of taxonomic considerations. Although a number of pollination syndromes have been identified in the southern African flora (Vogel, 1954), very few guilds have been described. The most striking of those that have been documented is the association

between the butterfly, *Aeropetes (Meneris) tulbaghia*, and late summer-flowering plant species with large bright red blossoms (Johnson & Bond, 1994).

Pollination by long-tongued flies is a relatively unusual phenomenon, first documented in southern Africa by Rudolf Marloth (1908) and later in somewhat more detail by Stefan Vogel (1954). Although pollination by long-tongued flies has also been reported in India (Fletcher & Son, 1931) and California (Grant & Grant, 1965), it appears to be particularly well developed only in southern Africa.

In the western part of southern Africa 28 species of Iridaceae and Geraniaceae have intensely colored purple to crimson flowers with extremely long floral tubes. These species all occur in a restricted geographic area, flower between July and September, and often occupy similar habitats. The conver-

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² Compton Herbarium, National Botanical Institute, Private Bag X7, Claremont 7735, South Africa.

³ B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166–0229, U.S.A.

gent floral morphology in this group of spring-flowering geophytes and small shrubs constitutes a distinct floral syndrome, and their coincident geography and phenology suggests that they are members of a specific pollination guild. Some of these species belong to the genus *Lapeirousia* (Iridaceae) and have already been found to be pollinated by one or both of two species of long-tongued flies in the genus *Prosoeca* (Diptera: Nemestrinidae) (Goldblatt et al., 1995). The purpose of this investigation is to extend our observations to determine whether the convergence in floral morphology to the *L. silenoides*-type flower in the other species coincides with pollination by the same fly species. Our results support the recognition of a distinct pollination guild. We discuss some of the implications of such a specialized pollination system on plant ecology and evolution and consider its possible origin.

METHODS

PLANT SPECIES

Members of the guild were initially identified during the course of field research in 1992 and 1993 in connection with a study of pollination ecology of *Lapeirousia* subg. *Lapeirousia* (Goldblatt et al., 1995). In this study species with purple to crimson flowers, white to cream nectar guides, and a perianth tube in excess of 30 mm were pollinated by *Prosoeca peringueyi* or *P. sp. nov.*, or occasionally both. We then reviewed the literature for records of species with purple to crimson flowers recorded from the west coast of southern Africa. All species having a perianth tube at least 30 mm long, or the anthers and stigmas held at least 30 mm from the base of the floral tube, were listed for further study. These species were examined in the field whenever possible to obtain observations on nectar characteristics and pollinators (Table 1). The apparent floral tube length was determined as the distance from base to the mouth of the tube. The actual floral tube length is less in some species due to the occlusion of the lower part of the tube and was determined empirically as the level down to which nectar could be freely extracted using a micropipette. Functional tube length was determined as actual tube length plus the distance between the mouth of the tube and the mid point of the anthers. Measurements were made on a minimum of 10 individuals per population.

Complete distribution ranges of plant species were taken from the literature and supplemented by recent herbarium records. Voucher specimens were made for all populations studied. Plant vouchers are deposited at the Missouri Botanical Garden

Herbarium, St. Louis (MO), and the Compton Herbarium, Cape Town (NBG).

INSECT SPECIES

Observations of insect foraging (Figs. 1–6) involved 4–20 hours per species and included such aspects as the density and diversity of floral foragers and how they removed rewards from flowers. Insects observed probing the floral tube or brushing the anthers or stigmas were captured and killed in a jar using ethyl acetate fumes. Location of pollen deposits was based first on visual observation of foraging insects and later on examination of pinned specimens. Individual insects were washed of pollen after pinning by placing the insect on a glass slide and rinsing the whole body in 100% ethanol while gently dislodging pollen loads on the frons, thorax, and sternum with a dissecting needle. The dry pollen residue was stained and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). To prevent contamination of the body of an insect with pollen carried by another in the same jar, the bodies of insect specimens were isolated from each other by wrapping them in tissue. Insect distributions were determined from collections at the Natal Museum, Pietermaritzburg, and the South African Museum, Cape Town, plus our own observations and collections. Insect vouchers are deposited at the Natal Museum, Pietermaritzburg.

NECTAR ANALYSES

Nectar volume measurements (Table 2) were made from unbagged flowers in the field and represent the standing crop that will be influenced by visitation rates. Whole flowers were picked and nectar was withdrawn from the base of the floral tube with 3 μ l capillary tubes after separating the ovary from the perianth (Iridaceae) or base of the hypanthium tube from the pedicel (Geraniaceae). Nectar was extracted from five or more individuals per population in most cases (Table 2). Nectar samples were dried on Whatmans filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for analysis (Table 2). The percentage of sucrose equivalents in fresh nectar was measured in the field on a Bellingham & Stanley handheld refractometer (0–50%) from five or more individuals per population.

RESULTS

PLANT CHARACTERISTICS

A total of 28 plant species occurring along the west coast and near interior of southern Africa, and

Table 1. Species belonging to the *Prosoeca peringueyi*-*P. sp.* pollination guild. Pollinators in parentheses are inferred on the basis of geography and pollinators of co-occurring plant species (*P. peringueyi* and *P. sp.* are not sympatric). Study sites and dates of observations on pollinators are listed for those species for which pollinator observations are available.

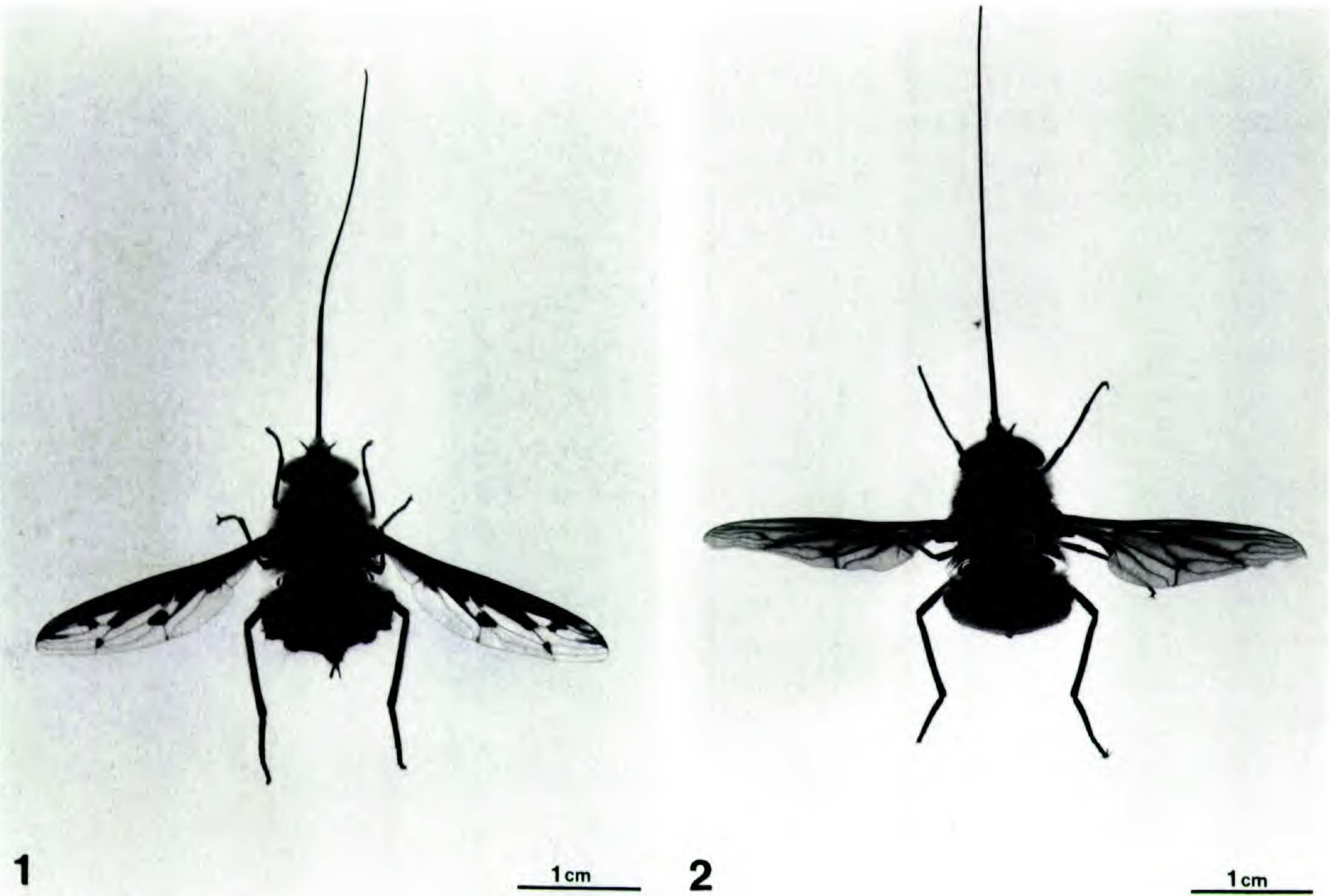
Family/species	Pollinator	Study site
Geraniaceae		
<i>Pelargonium</i>		
<i>cortusifolium</i> L'Herit.	(<i>P. peringueyi</i>)	
<i>crassicaule</i> L'Herit.	(<i>P. peringueyi</i>)	
<i>echinatum</i> Curt. (purple-flowered form)	(<i>P. peringueyi</i>)	
<i>incrassatum</i> (Andr.) Sims	<i>P. peringueyi</i>	Steinkopf-Anenous Pass (24 Aug. 1992); Kamieskroon (24 Aug. 1993); Garies Hill (23 Aug. 1994); Spektakel Mts. (5 Sep. 1994); Kamiesberg, Leliefontein (13 Sep. 1993 and 20 Sep. 1994)
<i>magenteum</i> van der Walt	<i>P. peringueyi</i>	Bidouw Valley (12 Aug. 1994)
<i>sericifolium</i> van der Walt	<i>P. peringueyi</i>	Steinkopf-Anenous Pass (24 Aug. 1992)
Iridaceae		
<i>Babiana</i>		
<i>curviscapa</i> G. Lewis	<i>P. peringueyi</i>	Spektakel-Naries (4 Sep. 1994)
<i>dregei</i> Baker	<i>P. peringueyi</i>	Kamiesberg, Sneekop (12 Sep. 1993); Kamiesberg, Leliefontein (13 Sep. 1993 and 20 Sep. 1994)
<i>ecklonii</i> Klatt	(<i>P. peringueyi</i>)	—
<i>flabellifolia</i> Harv. ex Klatt	<i>P. sp. nov.</i>	Hantamsberg Plateau (3 Sep. 1994)
<i>framesii</i> L. Bolus	<i>P. peringueyi</i> <i>P. sp. nov.</i>	Oorlogskloof Nature Reserve (8 Sep. 1993) Nieuwoudtville Nature Reserve (8 Sep. 1992 and 4 Sep. 1994)
<i>geniculata</i> G. Lewis	(<i>P. peringueyi</i>)	—
<i>pubescens</i> G. Lewis	<i>P. peringueyi</i>	Garies Hill (23 Aug. 1994)
<i>sambucina</i> var.		
<i>longibracteata</i> G. Lewis	(<i>P. sp.</i>)	—
<i>unguiculata</i> G. Lewis	(<i>P. peringueyi</i>)	—
<i>Geissorhiza</i>		
<i>kamiesmontana</i> Goldblatt	(<i>P. peringueyi</i>)	—
<i>Hesperantha</i>		
<i>latifolia</i> (Klatt) de Vos	<i>P. peringueyi</i>	Kamiesberg, Sneekop (12 Sep. 1993)
<i>oligantha</i> Diels	(<i>P. sp.</i>)	—
<i>purpurea</i> Goldblatt	(<i>P. peringueyi</i>)	—
<i>Lapeirousia</i>		
<i>dolomitica</i> subsp.		
<i>dolomitica</i> Dinter	<i>P. peringueyi</i>	Anenous Hills (24 Aug. 1992)
<i>lewisiana</i> (B. Nord.) Goldblatt	(<i>P. peringueyi</i>)	—
<i>jacquinii</i> N. E. Br.	<i>P. sp. nov.</i>	Oorlogskloof Farm (8 Sep. 1992); Oorlogskloof Nature Reserve (8 Sep. 1992)
	<i>P. peringueyi</i>	Botterkloof Pass (23 Aug. 1993); Farm Alpha (1 Sep. 1994)
<i>oreogena</i> Schltr.	<i>P. sp. nov.</i>	Glenlyon (23 Aug. 1993 and 4 Sep. 1994); Nieuwoudtville Nature Reserve (4 Sep. 1994)
<i>pyramidalis</i> subsp.		
<i>regalis</i> Goldblatt & J. Manning	<i>P. peringueyi</i>	Trawal (5 and 11 Aug. 1994)
<i>silenoides</i> (Jacq.) Ker-Gawl.	<i>P. peringueyi</i>	Spektakel Pass (23 Aug. 1992); Kamieskroon to Grotvlei (22 Aug. 1992); Kamieskroon (2 Aug. 1993); 10 km S Kamieskroon (24 Aug. 1993); Garies Hill (23 Aug. 1994)
<i>violacea</i> Goldblatt	<i>P. peringueyi</i>	Botterkloof Pass (23 Aug. 1993)

Table 1. Continued.

Family/species	Pollinator	Study site
<i>Romulea</i> <i>hantamensis</i> (Diels) Goldblatt	<i>P. sp. nov.</i>	Hantamsberg (3 Sep. 1994)
<i>Sparaxis</i> <i>variegata</i> subsp. <i>metelerkampiae</i> (L. Bolus) Goldblatt	<i>P. peringueyi</i>	Pakhuis Mts., Farm Alpha (1 Sep. 1994)
<i>Tritonia</i> <i>marlothii</i> de Vos	(<i>P. peringueyi</i>)	—
<i>Xenoscapa</i> <i>uliginosa</i> Goldblatt & J. Manning	(<i>P. peringueyi</i>)	—

mostly endemic there, were identified as converging on *Lapeirousia silenoides* in floral morphology (Table 3). These include 22 species of Iridaceae in the genera *Babiana*, *Geissorhiza*, *Hesperantha*, *Lapeirousia*, *Romulea*, *Sparaxis*, *Tritonia*, and *Xenoscapa*, and six species of Geraniaceae, all in the genus *Pelargonium*. Within this group are seasonal geophytes (Iridaceae and *Pelargonium incrassatum*) and small to moderate-sized shrubs (*Pelargonium cortusifolium*, *P. crassicaule*, *P. echinatum*, *P. ma-*

genteum, and *P. sericifolium*). While the habits and growth forms of the species vary, their flowers share several unusual properties and may be considered to constitute a distinct floral syndrome (Figs. 7–9). The floral tube is straight or slightly curved to sigmoid, very narrow (1.5–2.5 mm diam.), and (18–) 30–70 mm long, and the petals or tepals are shorter than the tube. The flowers are typically zygomorphic, with stamens and styles unilateral, but are actinomorphic in five species in which the stamens are sym-



Figures 1, 2. The *Prosoeca* species responsible for pollinating plant species with the *Lapeirousia silenoides*-type flower.—1. *P. peringueyi*.—2. *P. sp. nov.*



Figures 3–6. *Prosoeca* species foraging on *Lapeirousia silenoides*-type flowers. In these photographs the flies are inserting their mouthparts into the floral tubes and have not yet probed deep enough to reach the nectar in the lower part of the tube or brush the anthers and stigmas of the flowers.—3. *P. peringueyi* visiting *L. pyramidalis* subsp. *regalis*.—4. *P. peringueyi* visiting *Babiana dregei*.—5. *P. peringueyi* and *L. silenoides*.—6. *P. sp. nov.* and *L. oreogena*.

Table 2. Nectar characteristics of species with the *Lapeirousia silenoides*-type flower. Fru = fructose, Glu = glucose, Suc = sucrose. Sample size for nectar volume figures are indicated in parentheses in volume column; sample size for nectar sugar components is in the last column after sucrose:fructose + glucose ratio.

Family/species	Volume μl (n)	Mean % sugar	Fru	Glu	Suc	Mean Suc/ Glu + Fru (n)
Geraniaceae						
<i>Pelargonium</i>						
<i>cortusifolium</i>	2.6–3.1 (2)	24	—	—	—	—
<i>incrassatum</i>	1.5–2.2 (1)	38	0	75	25	0.33 (1)
<i>magenteum</i>	0.6–1.8 (5)	29	38	40	22	0.28 (1)
<i>sericifolium</i>	no measurable nectar produced					
Iridaceae						
<i>Babiana</i>						
<i>curviscapa</i>	2.0–4.4 (5)	25	12	19	69	2.23 (1)
<i>dregei</i>	3.9–9.6 (5)	22	13–15	19–21	64–68	1.94 (2)
<i>ecklonii</i>	4.3–8.9 (5)	27.7	5–11	10–18	72–85	3.29 (3)
<i>flabellifolia</i>	3.9–9.6 (5)	27	7	14	79	3.76 (1)
<i>framesii</i>	2.6–6.4 (5)	26	7–9	12–14	77–81	3.84 (3)
<i>geniculata</i>	3.2–4.8 (5)	29	17	21	62	1.63 (1)
<i>pubescens</i>	3.2–4.8 (5)	28	3–8	9–14	78–88	2.18 (2)
<i>sambucina</i>						
var. <i>longibracteata</i>	3.9–6.6 (3)	30	6–12	10–19	69–84	3.48 (3)
<i>Hesperantha</i>						
<i>latifolia</i>	0.7–1.1 (10)	24	23–29	24–30	41–53	0.94 (3)
<i>oligantha</i>	1.1–1.8 (5)	26.4	19–23	24–25	52–57	1.20 (2)
<i>Lapeirousia</i>						
<i>dolomitica</i>						
subsp. <i>dolomitica</i>	1.4–5.5 (5)	29	4–9	12–14	77–84	4.13 (2)
subsp. <i>lewisiana</i>	5.1–5.5 (4)	27	5–12	14–25	63–81	2.94 (5)
<i>jacquinii</i>	1.5–2.3 (6)	26	8	17	75	3.00 (1)
<i>oreogena</i>	2.5–7.3 (10)	26	13	21.5	65.5	1.90 (4)
<i>pyramidalis</i>						
subsp. <i>regalis</i>	2.6–4.8 (10)	28	4–21	12–31	48–84	2.45 (6)
<i>silenoides</i>	1.7–3.6 (16)	27	5–8	18–27	65–77	2.45 (3)
<i>violacea</i>	1.4–1.8 (10)	27	9–13	15–16	71–76	2.77 (2)
<i>Romulea</i>						
<i>hantamensis</i>	3.7–5.2 (3)	20	23	27	50	1.00 (1)
<i>Sparaxis</i>						
<i>variegata</i> subsp.						
<i>metelerkampiae</i>	1.7–2.2 (6)	28.5	1–12	4–22	70–95	3.23 (4)
<i>Tritonia</i>						
<i>marlothii</i>	1.8–3.5 (5)	29	13–14	17–18	68–70	2.23 (2)

metrically arranged around a central style (Table 3). In all species except *Pelargonium sericifolium* (which does not produce nectar; Goldblatt et al., 1995), nectar accumulates at the base of the floral tube and fills its lower third. Nectar is thus accessible only to insects with tongues long enough to reach at least into the lower third of the tube.

The flowers are mostly intensely pigmented in colors ranging from dark blue-purple and violet to bright red-purple or cerise, but are pale mauve in taxa from the Richtersveld (northern Namaqualand) and southern Namibia. Contrasting markings in white or cream are almost always present, usually

accompanied by additional darker areas of pigmentation (Figs. 7–9). The markings, which may take the form of streaks or spots near the tepal bases in species of Iridaceae, are confined to the lower tepals in species with zygomorphic flowers but are present on all the tepals in species with actinomorphic flowers. In *Pelargonium* (Fig. 7) the pale color signal is provided by the white filaments, which are unilateral and declinate, rather than by tepal coloring. Whatever the shape and color of the flowers, the anthers and stigmatic surfaces are always held outside the mouth of the floral tube in a position where they will be brushed by the body of an insect probing the

Table 3. Floral characteristics of species with the *Lapeirousia silenoides*-type flower. The floral tube is closed in the lower 10–12 mm in *B. curviscapa*, 20–30 mm in *B. dregei*, and 15–20 mm in *B. framesii*, hence floral tube length does not reflect the distance that an insect must extend its mouthparts to reach the nectar. Z = zygomorphic; A = actinomorphic.

Family/species	Symmetry	Scent	Tube length (mm)	Flowering time
Geraniaceae				
<i>Pelargonium</i>				
<i>cortusifolium</i>	Z	0	ca. 30	Mar.–Nov.
<i>crassicaule</i>	Z	0	15–25	(Mar.–)Aug.–Sep.(–Oct.)
<i>echinatum</i>	Z	0	25–55	(July–)Aug.–Oct.
<i>incrassatum</i>	Z	0	30–40	Aug.–Sep.
<i>magenteum</i>	Z	0	33–47	(June–)July–Sep.
<i>sericifolium</i>	Z	0	35–60	(July–)Aug.–Sep.
Iridaceae				
<i>Babiana</i>				
<i>curviscapa</i>	Z	0	36–48	Aug.–Sep.
<i>dregei</i>	Z	0	50–65	Aug.–Sep.
<i>ecklonii</i>	Z	0	40–50	Sep.
<i>flabellifolia</i>	Z	0	40–65	Aug.–Sep.
<i>framesii</i>	Z	1	60–70	Aug.–Sep.
<i>geniculata</i>	Z	0	35–45	Aug.
<i>pubescens</i>	Z	0	ca. 50	(July–)Aug.
<i>sambucina</i>				
var. <i>longibracteata</i>	Z	1	30–50	Aug.–Sep.
var. <i>unguiculata</i>	Z	1	38–55	Aug.–Sep.
<i>Geissorhiza</i>				
<i>kamiesmontana</i>	Z	0	18–25	Sep.
<i>Hesperantha</i>				
<i>latifolia</i>	A	0	15–25	Aug.–Sep.
<i>oligantha</i>	A	0	30–36	Sep.(–Oct.)
<i>purpurea</i>	A	0	ca. 20	Sep.
<i>Lapeirousia</i>				
<i>dolomitica</i>				
subsp. <i>dolomitica</i>	Z	1	25–45	(June–)July–Sep.
subsp. <i>lewisiana</i>	Z	0	45–55	July–Aug.
<i>jacquinii</i>	Z	0	30–40	July–Sep.
<i>oreogena</i>	A	0	50–60	Aug.(–Sep.)
<i>pyramidalis</i>				
subsp. <i>regalis</i>	Z	0	40–50	July–Aug.
<i>silenoides</i>	Z	0	40–55	July–Sep.
<i>violacea</i>	Z	0	35–40	Aug.–Sep.
<i>Romulea</i>				
<i>hantamensis</i>	A	0	50–70	Aug.–Sep.
<i>Sparaxis</i>				
<i>variegata</i>				
subsp. <i>metelerkampiae</i>	Z	0	34–37	Aug.–Sep.
<i>Tritonia</i>				
<i>marlothii</i>	Z	0	25–44	Aug.–Sep.
<i>Xenoscapa</i>				
<i>uliginosa</i>	Z	0	25–30	Sep.(–Oct.)

tube. Pollen is often inconspicuous and of the same color as the tepals, especially in *Lapeirousia*, or may be white, possibly adding to the signal provided by the contrasting color of the perianth. In *P. incrassatum* and *P. magenteum* the pollen is bright orange.

We have no data on ultra-violet light reflectance in any of the species under consideration; and it is possible that differential reflectance in the UV light range may add to the visual signals evident in the visible range.

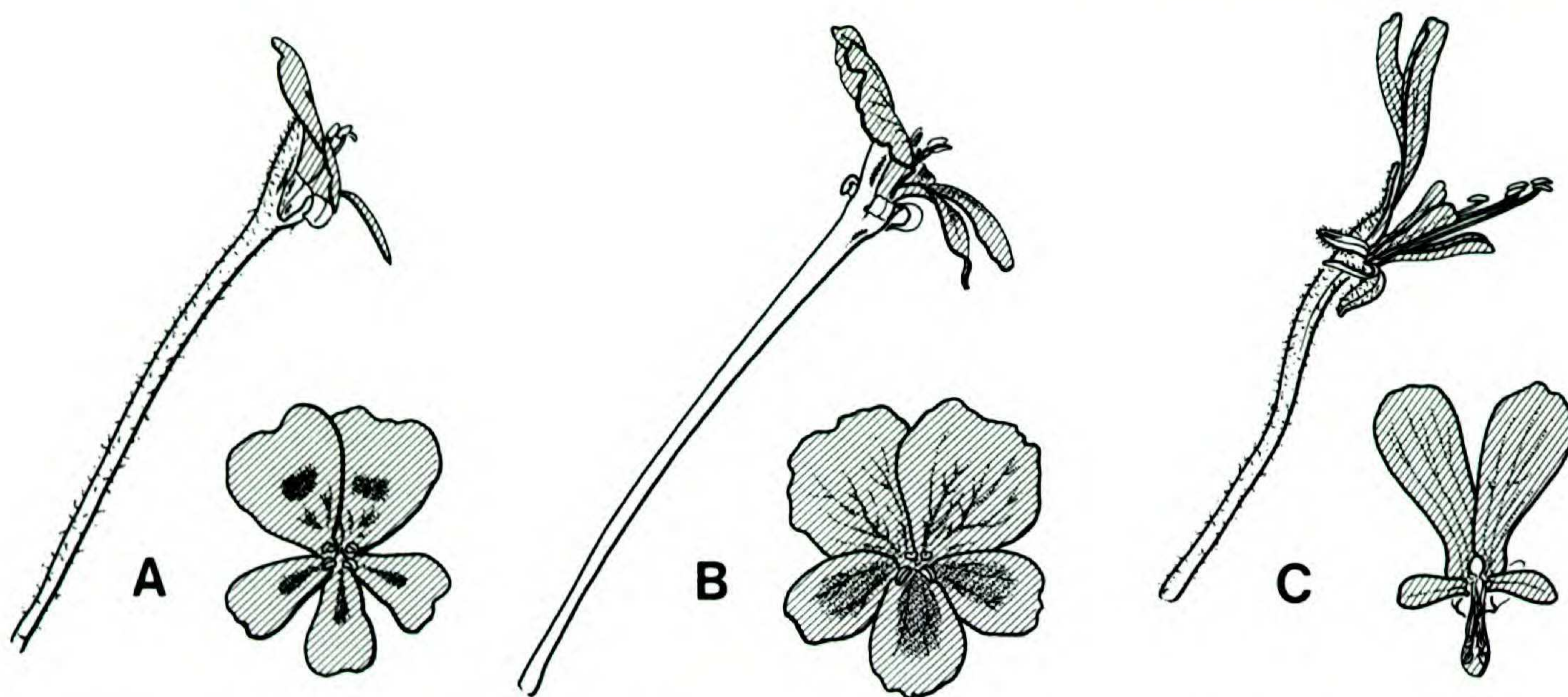


Figure 7. Flowers of species of Geraniaceae belonging to the *Lapeirousia silenoides* guild, all pollinated by *Prosoeca peringueyi*.—A. *Pelargonium magenteum*.—B. *P. sericifolium*.—C. *P. incrassatum*. (Scale: full size.)

Flowers open during the day and often close partially or fully at night. They are typically unscented, at least to the human nose both in the open air and when several flowers are held in a warm confined space. Some species of *Babiana*, however, have a light to moderately strong scent (Table 3). The flowering season in the guild ranges from late May (one species), with a marked rise in July and a peak in early September, and continues until early October (Fig. 10). Individual species and populations remain in flower for at least two weeks, or for a considerably longer time in the case of the shrubby *Pelargonium* species. Individual flowers usually last three to four days, and longer in species of Iridaceae when not pollinated. Species of Iridaceae are protandrous. The pollen is shed half a day to one day before the stigmas unfold and become available for pollen deposition. Unless removed by some agent, the pollen remains in place in the anther thecae. Species of *Pelargonium* are also protandrous. The deciduous anthers are shed the same day that the flower opens, whereas the stigmas only unfold the following day. Flowers of the species of the guild are almost all herkogamous (and self-incompatible, at least in *L. dolomitica* and *L. silenoides*) and thus require insect-mediated pollination. The only known exception is *L. jacquinii*, which is self-compatible and autogamous (Goldblatt et al., 1995).

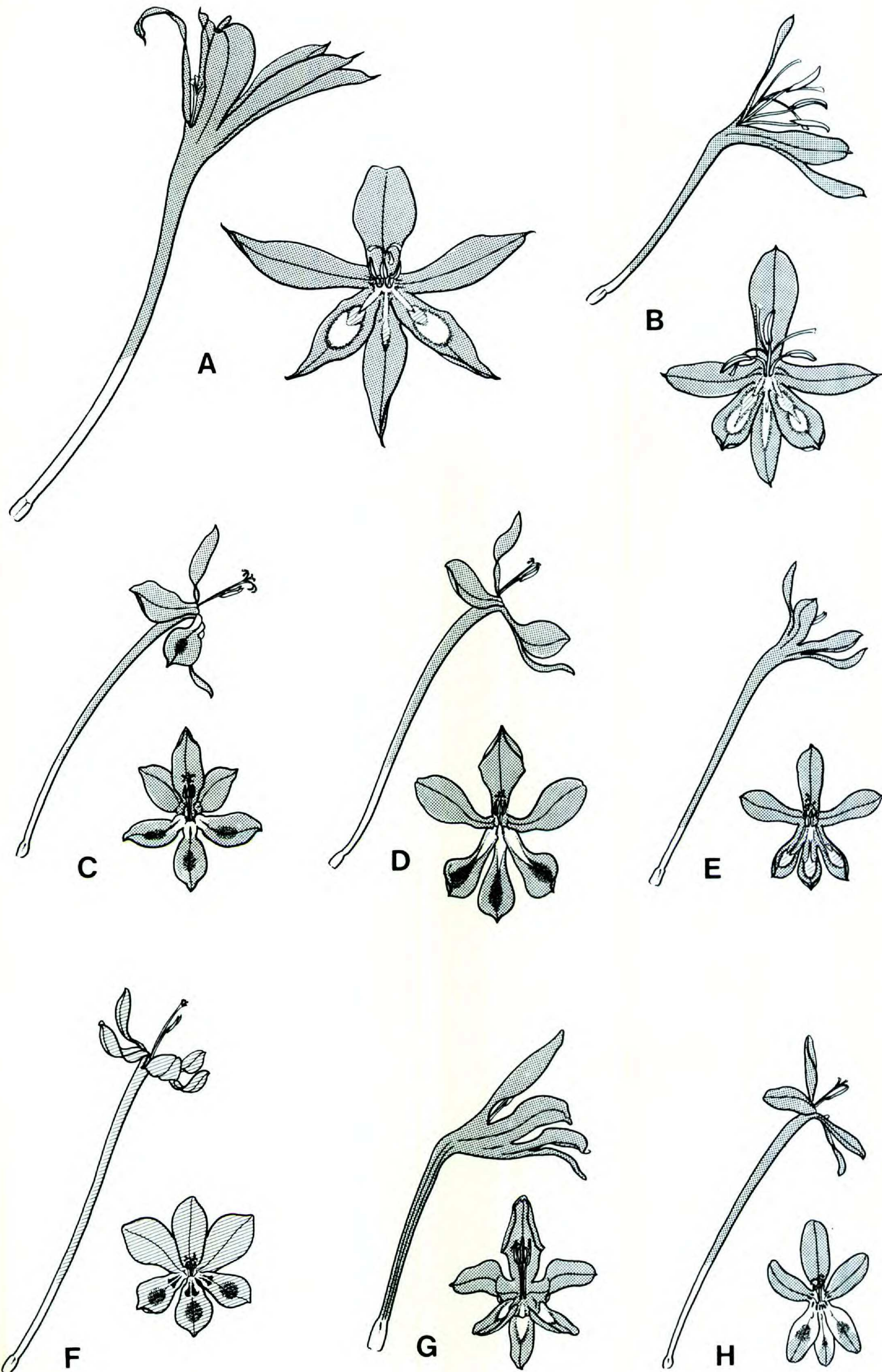
Nectar quantities are ample, and the upper range of nectar volumes for species in the guild is 1.1 μl to 9.6 μl (Table 2). Nectar sugar concentrations are mostly 24–30%, exceptionally as low as 20% in *Romulea hantamensis* and 22% in *Babiana dregei* (Table 2). Nectar sugar analyses, available for 21 species (Table 2), show a characteristic sucrose-rich to sucrose-dominant pattern in the 15 species of Iridaceae examined. Sucrose:hexose sugar ratios range from a high of 4.13 in *Lapeirousia dolomitica* subsp. *dolomitica* to 1.20 and 0.94 in the two species of *Hesperantha* for which we have data, and 1.00 in *Romulea hantamensis*, the only species of that genus belonging to the guild. Most species have sucrose:hexose ratios in the 2 to 3.5 range. The pattern in two species of *Pelargonium*, however, shows hexose dominance with sucrose:hexose ratios of 0.28 and 0.33. This is a marked contrast to the spectrum for Iridaceae.

POLLINATOR IDENTITY

Pollinator observations were obtained for 17 out of the total listing of 28 plant species (Table 4). These species are from throughout the range occupied by members of the guild. In all of these instances pollination was carried out by either *Prosoeca peringueyi* or *P. sp.*, or, rarely, both (Figs. 1, 2). No other insects were seen to visit any of the

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Figure 8. Flowers of species of Iridaceae belonging to the *Lapeirousia silenoides* guild pollinated (or inferred to be pollinated) by *Prosoeca peringueyi*.—A. *Babiana framesii*.—B. *B. curviscapa*.—C. *Lapeirousia pyramidalis* subsp. *regalis*.—D. *L. dolomitica* subsp. *dolomitica*.—E. *L. violacea*.—F. *L. silenoides*.—G. *Sparaxis variegata* subsp. *metelkampiae*.—H. *Tritonia marlothii*. (Scale: full size.)



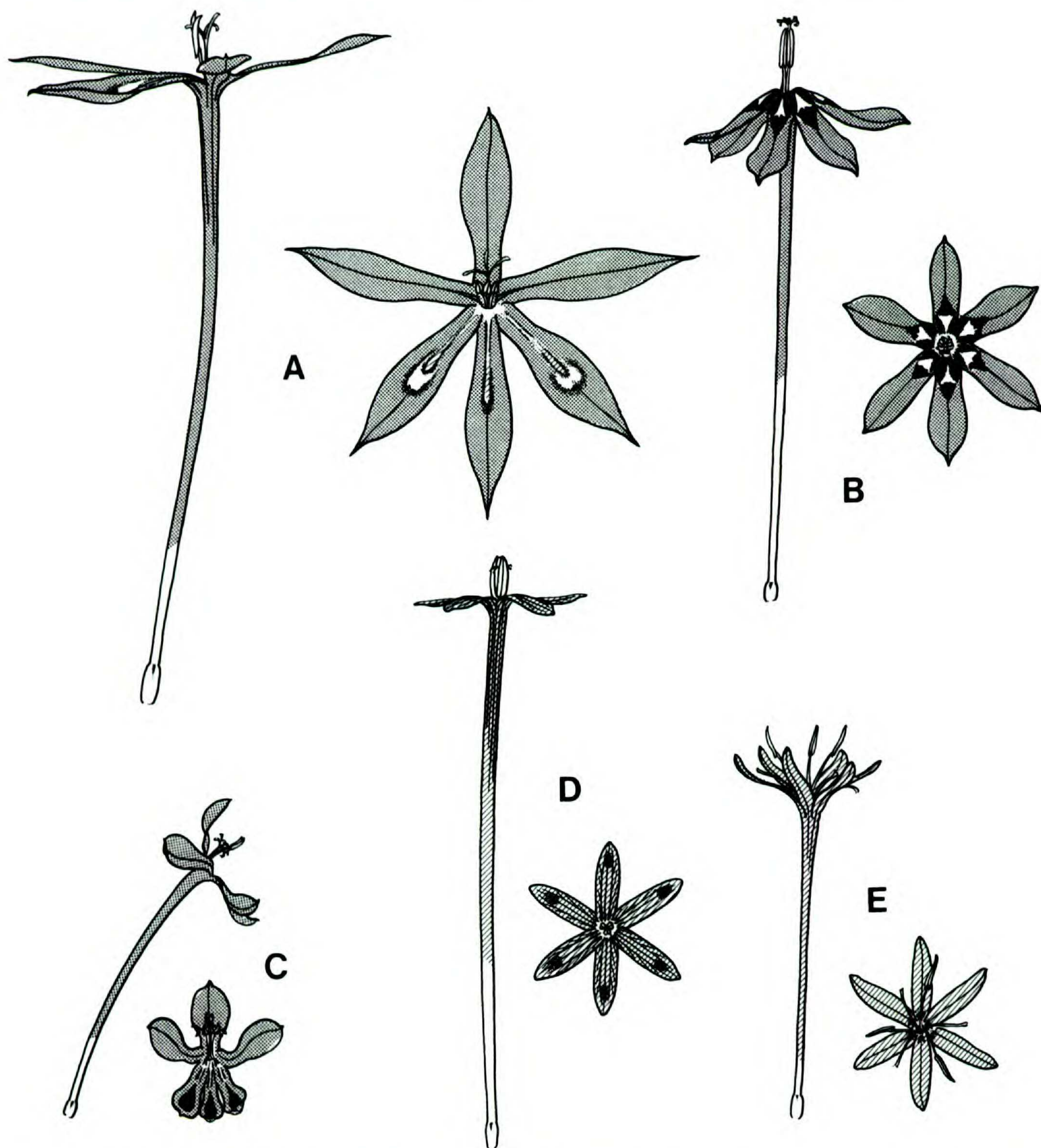


Figure 9. Flowers of species of Iridaceae belonging to the *Lapeirousia silenoides* guild pollinated (or inferred to be pollinated) by *Prosoeca* sp. nov.—A. *Babiana flabellifolia*.—B. *Lapeirousia oreogena*.—C. *L. jacquinii*.—D. *Romulea hantamensis*.—E. *Hesperantha oligantha*. (Scale: full size.)

species of the guild during more than 200 hours of observation time except for three anthophorid bees, which visited but did not forage on individuals of *L. silenoides*. It is almost certain that the plant species for which we do not have pollinator observations will prove to be one or both of these fly species. Because the fly species are allopatric, we have inferred pollinator identity on the basis of the range of the plant species for which we have no observations. *Prosoeca peringueyi* is confirmed as the primary pollinator of three species of Geraniaceae and

eleven species of Iridaceae, and *P. sp.* of five species of Iridaceae (Table 4).

GEOGRAPHY

The plant species with the *Lapeirousia silenoides*-type flowers are restricted to coastal and near interior southern Africa, a semiarid region of low, predominantly winter rainfall. The 28 species have a collective range that extends from extreme southwestern Namibia through the western part of North-

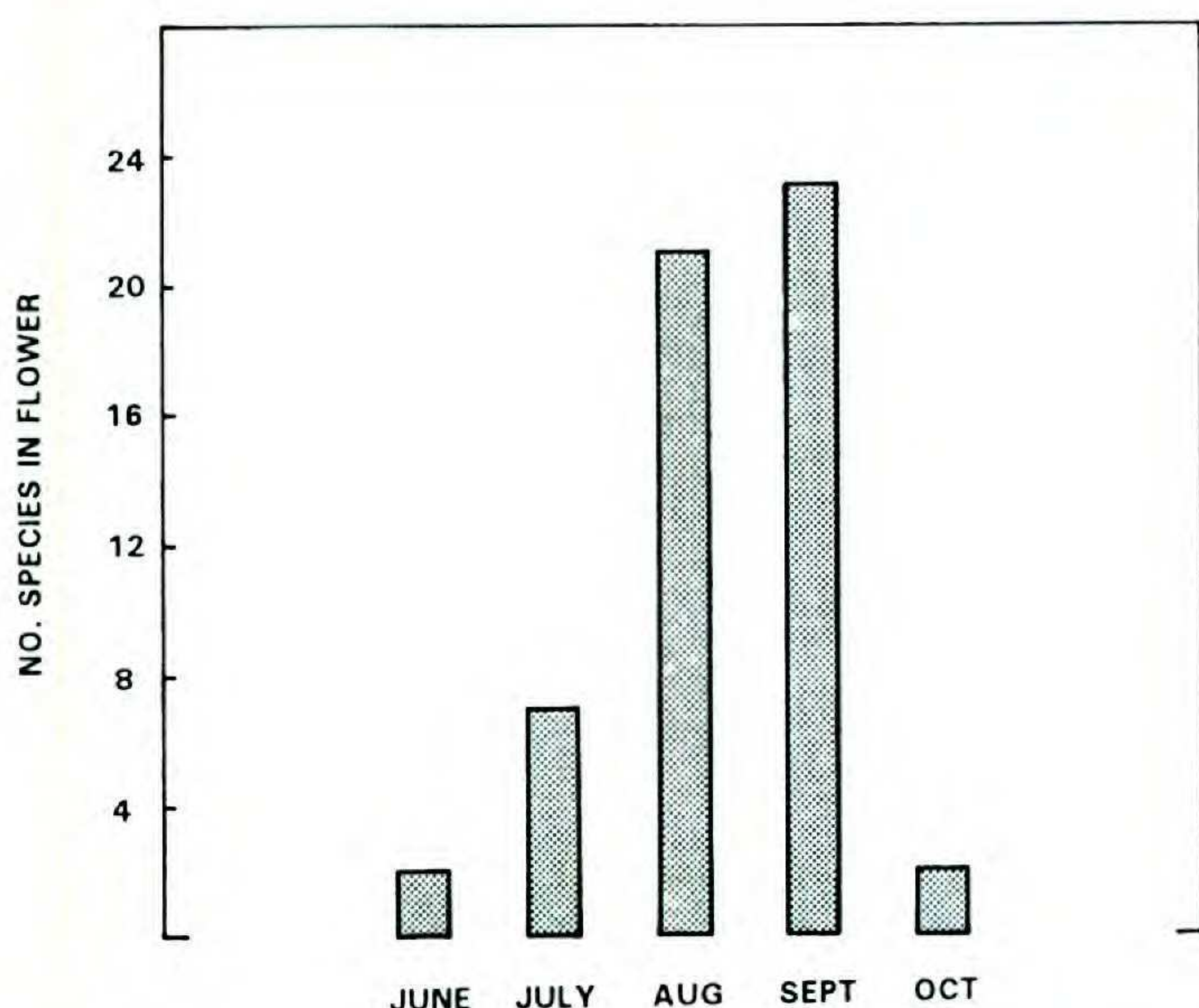


Figure 10. Flowering times of the plant species belonging to the *Lapeirousia silenoides* guild.

ern Cape Province, South Africa, an area known as Namaqualand, and reaches the northwestern portion of Western Cape Province (Fig. 11). The distribution of individual species within this area is often highly local (Goldblatt, 1972, 1984, 1985; Lewis, 1959; van der Walt & Vorster, 1988). At most, seven species of the guild are present in any quarter-degree square, and no more than four guild members co-occur locally. Diversity is greatest in the Kamieskroon area of Namaqualand and in the Pakhuis Mountains of Western Cape Province. Usually the ranges of two or more species overlap. Up to seven species have been recorded in a quarter-degree square of geographical latitude and longitude. Species are infrequent in the north of the range, where only *L. dolomitica* subsp. *dolomitica*, *Tritonia marlothii*, *Pelargonium cortusifolium*, and *P. crassicaule* occur, and along the coast where the putatively autogamous *L. jacquinii* is the only representative.

The combined ranges of *Prosoeca peringueyi* and *P. sp.* (Fig. 12) fall entirely within the main range of the plant species and accord almost exactly with the area within which two or more plant species occur. *Prosoeca peringueyi* has the wider distribution, extending from northern Namaqualand to the Pakhuis Mountains, and *P. sp.* has a localized range along a corridor of high country in Northern Cape Province between Nieuwoudtville and the Hantam Mountains.

POLLEN PLACEMENT

Observation of living and pinned insects, corroborated by pollen washes, confirmed that pollen of a particular plant species is consistently deposited on a limited part of the insect's body (Table 4). We

have identified four mutually exclusive sites of deposition: top of the thorax or dorsum; top of the head or frons; the base of the proboscis or face; and underside of the thorax or sternum and abdomen (Fig. 13). *Pelargonium* flowers have declinate stamens so that the filaments and anthers are situated below the mouth of the floral tube (Fig. 7) and pollen deposition is invariably sternotribic. In *P. incrassatum* (Fig. 7C), which has long filaments, pollen is deposited on the underside of the sternum and thorax (Fig. 13D), but in *P. sericifolium* and *P. magenteum* (Fig. 7A, B, 13C), which have very short filaments, deposition is on the face. Species of Iridaceae belonging to the guild have either actinomorphic flowers with symmetrically disposed stamens (Fig. 9B, D, E) or zygomorphic flowers with the stamens unilateral and arcuate (Figs. 8, 9A, C). The anthers are then either held above the mouth of the floral tube or are dorsal to it, and pollen deposition is nototribic (Fig. 13A, B). Filament length is also variable, being short in species of *Lapeirousia* and *Romulea* but relatively long in *Babiana*, and the site of pollen deposition varies accordingly. In species of *Babiana* pollen deposition is mostly on the top of the thorax (in one species on the top and sides), in *Hesperantha* on the ventral head, whereas in *Lapeirousia* and *Romulea* it is on the frons.

Often there are at least two species of the guild, and sometimes more, co-blooming locally and visited indiscriminately by *P. peringueyi*. At such sites, particularly in Namaqualand, *Lapeirousia silenoides*, *Pelargonium incrassatum*, and one species of *Babiana*, either *B. curviscapa*, *B. dregei*, *B. framesii*, or *B. pubescens*, flower together. In the Clanwilliam District *L. jacquinii*, sometimes *L. violacea*, *Pelargonium magenteum*, and a species of *Babiana* and/or *Sparaxis* commonly form part of a local plant community. At sites in the Kamiesberg, central Namaqualand, as many as four co-blooming members of the guild were recorded. *Lapeirousia silenoides*, *B. curviscapa*, *Hesperantha latifolia*, and *Pelargonium incrassatum* were noted near Leliefontein, and on Sneekop we encountered *Babiana dregei*, *H. latifolia*, and two other presumed members of the guild, *Xenoscapa uliginosa* (endemic there) and *Geissorhiza kamiesbergensis*.

A similar situation prevails with species visited by *Prosoeca sp. nov.* At different sites *Babiana framesii* and either *Lapeirousia oreogena* or *L. jacquinii*, or *L. jacquinii* and *B. sambucina*, or *B. flabelifolia*, *Hesperantha oligantha*, and *Romulea hantamensis* flower concurrently and are visited indiscriminately by the same fly individual. In the above examples, pollen contamination of one spe-

Table 4. Pollinator characteristics and effective tube length of species with the *Lapeirousia silenoides*-type flower. Measurements of insect mouthparts were made from individuals collected on the plant species concerned. Dash in column three reflects no pollinator recorded on that species.

Family/species	Anther to base of tube (mm)	Pollen deposition site	Insect tongue length (mm)
Plants pollinated (or inferred to be pollinated) by <i>Prosoeca peringueyi</i>			
Geraniaceae			
<i>Pelargonium</i>			
<i>cortusifolium</i>	ca. 35	ventral head	—
<i>crassicaule</i>	18–35	ventral head	—
<i>echinatum</i>	30–58	ventral head	—
<i>incrassatum</i>	44–52	ventral thorax	28–33
<i>magenteum</i>	37–53	ventral head	30–35
<i>sericifolium</i>	43–66	ventral head	35–40
Iridaceae			
<i>Babiana</i>			
<i>curviscapa</i>	40–55	dorsal thorax	25–28
<i>dregei</i>	47–53	dorsal thorax	25–28
<i>ecklonii</i>	52–65	dorsal thorax	—
<i>framesii</i>	45–50	dorsal thorax	30–35
<i>geniculata</i>	45–55	dorsal thorax	—
<i>pubescens</i>	ca. 62	dorsal thorax	32–35
<i>sambucina</i>			
var. <i>unguiculata</i>	38–55	dorsal thorax	—
<i>Geissorhiza</i>			
<i>kamiesmontana</i>	23–32	ventral head	—
<i>Hesperantha</i>			
<i>latifolia</i>	20–35	ventral head	20–25
<i>purpurea</i>	ca. 25	ventral head	—
<i>Lapeirousia</i>			
<i>dolomitica</i>			
subsp. <i>dolomitica</i>	25–45	frons	30
subsp. <i>lewisiana</i>	40–50	frons	—
<i>jacquinii</i>	35–45	frons	32–35
<i>pyramidalis</i>			
subsp. <i>regalis</i>	45–55	frons	32–34
<i>silenoides</i>	45–60	frons	35–40
<i>violacea</i>	40–45	frons	32–35
<i>Sparaxis</i>			
<i>variegata</i>			
subsp. <i>metelerkampiae</i>	40–45	frons	32–35
<i>Tritonia</i>			
<i>marlothii</i>	27–46	frons	—
<i>Xenoscapa</i>			
<i>uliginosa</i>	27–32	frons	—
Plants pollinated (or inferred to be pollinated) by <i>Prosoeca</i> sp. nov.			
Iridaceae			
<i>Babiana</i>			
<i>flabellifolia</i>	50–70	frons	40–45
<i>framesii</i>	45–50	dorsal thorax	40–48
<i>sambucina</i>			
var. <i>longibracteata</i>	35–55	dorsal thorax	—
<i>Hesperantha</i>			
<i>oligantha</i>	30–40	ventral head	—
<i>Lapeirousia</i>			
<i>jacquinii</i>	35–45	frons	40–45
<i>oreogena</i>	55–65	ventral head	40–48
<i>Romulea</i>			
<i>hantamensis</i>	60–75	frons	40–45

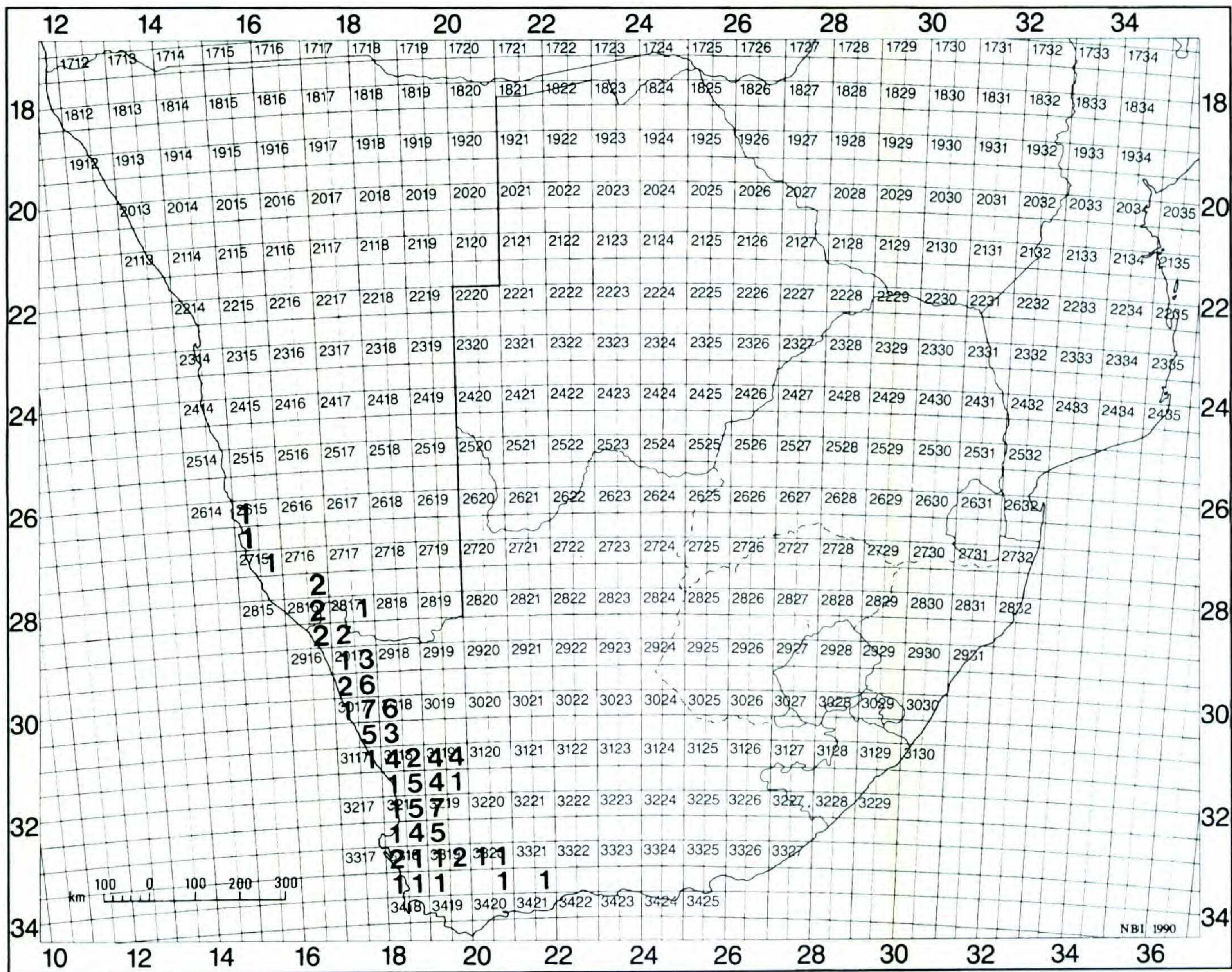


Figure 11. Map of southern Africa showing the distribution range of species with the *Lapeirousia silenoides*-type flower. Figures indicate the total number of species recorded per quarter-degree square of geographical latitude and longitude.

cies by that of another is minimized or prevented by the use of different deposition sites as outlined above. At any study site that included two or more species of the guild, the pollen of each species was placed on a different part of an insect's body (e.g., Fig. 13). The only exception to this pattern was at Botterkloof Pass (and presumably other localities where these two species co-occur) where pollen deposition sites for *Lapeirousia jacquinii* and *L. violacea* are identical.

A crude estimate of potential pollen contamination was determined by comparing the number of guild members recorded from any quarter-degree square with the number of pollen deposition sites utilized by these species. The number of placement positions exploited in any quarter-degree square is positively correlated with the total number of guild members occurring in that grid (Fig. 14). A coefficient of pollen contamination was calculated for grids containing more than one species of the guild by dividing the number of species into the number of loading sites per quarter-degree grid. For the

species in the guild the mean coefficient was 0.77, suggesting selection for reduced pollen contamination. The index greatly underestimates the pollen contamination coefficient because not all of the species in a grid co-occur locally. The local co-occurrence of more than one species using the same pollen deposition site is rare, and we only know of the single example mentioned above.

FORAGING PATTERNS

Adult specimens of *Prosoeca peringueyi* have been collected from late July to late September, with a peak during mid August to mid September. Specimens of *P. sp.* have only been recorded from mid August to mid September. Both species have a similar foraging behavior. The flies move rapidly between flowers and hover for two to three seconds while orienting and inserting their proboscis into the floral tube (Goldblatt et al., 1995) (Figs. 3–6). In species with zygomorphic flowers the fly always orients itself in the same way, approaching the flow-

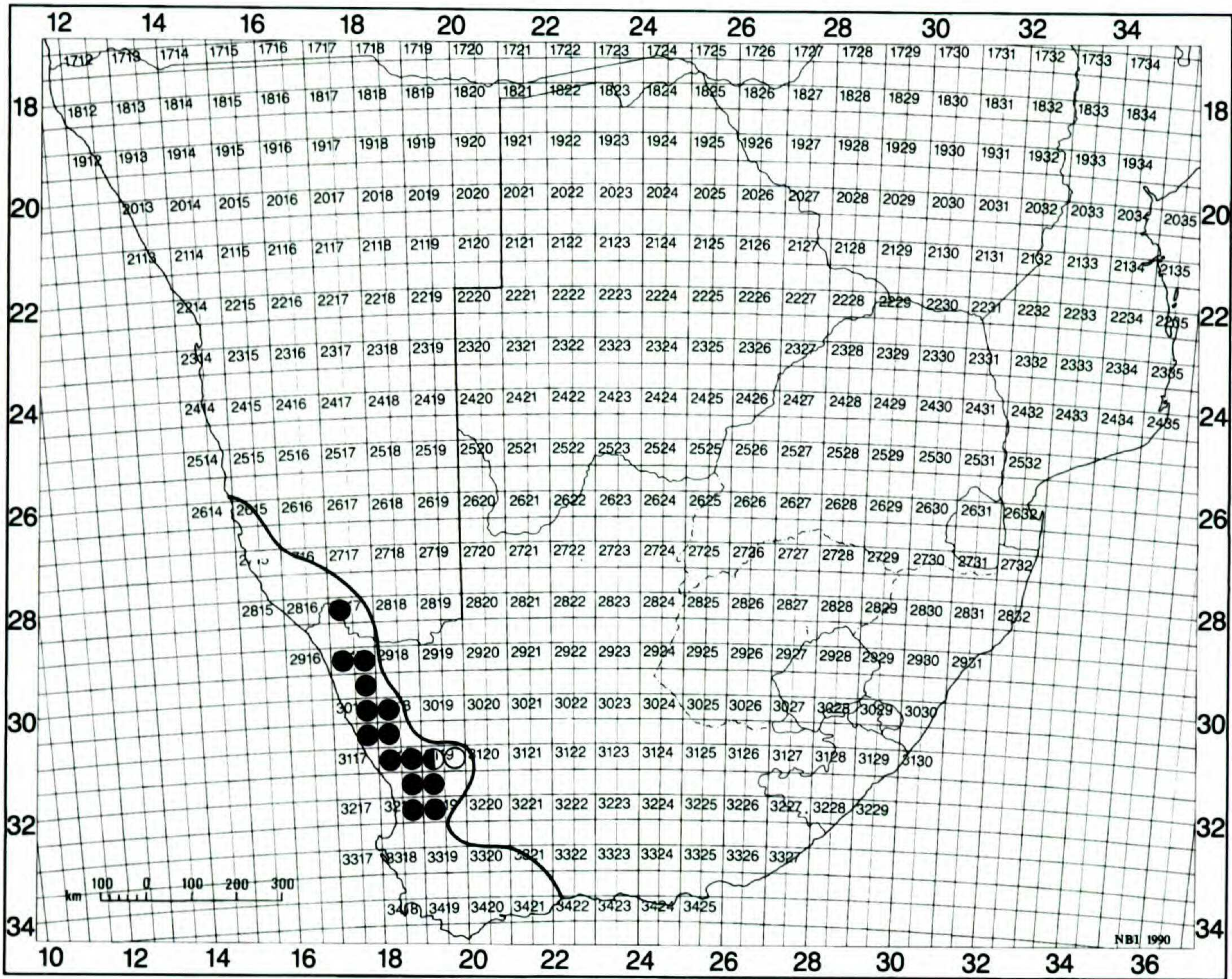


Figure 12. Map of southern Africa showing the distribution ranges of *Prosoeca peringueyi* (closed circles) and *P. sp.* (open circles) recorded on quarter-degree squares of latitude and longitude. The combined ranges of plant species belonging to the guild pollinated by these two fly species is indicated by the heavy outline.

er directly from the front. The flies are unable to discriminate between flowers that have already been visited either by themselves by other individuals and may repeatedly visit the same flower even when all the nectar has been removed (pers. obs.). When nectar is absent visits are brief.

Both fly species are active on mild to warm days from mid morning to early afternoon, and again in the late afternoon. Foraging is most active on warm days between 12:30 and 2:30 PM, but some foraging occurs at almost any time of day. Density of visitors varies considerably, ranging from 4 to 5 flies present locally at the same time, or as few as 1 or 2 over periods as long as an hour. Flies remain at each flower for 3–5 seconds, and pollen is passively brushed onto various parts of the head, thorax, or abdomen, depending on the species visited. Pollen depositions are usually heavy enough to be visible to the naked eye against the dark bodies of the insects. Commonly, pollen of two or three different species can be distinguished by color, that

of each species located on a different part of the body.

DISCUSSION

THE LAPEIROUSIA SILENOIDES-TYPE FLORAL SYNDROME

Our observations indicate that plants with flowers conforming to the following syndrome constitute a guild adapted for pollination by the long-proboscid flies, *Prosoeca peringueyi* and *P. sp. nov.*: perianth or hypanthium tube narrow, straight or slightly curved, and 30–60 mm long; tepals or petals short in relation to tube length and pigmented dark purple to crimson, or sometimes lilac or pale mauve, with nectar guides consisting of white to cream spots and streaks and areas of darker pigmentation; and exerted and prominent anthers and stigmas that are presented outside the mouth of the tube so that they will contact the body of any animal that probes the floral tube. Associated with these features is the production of nectar with a relatively

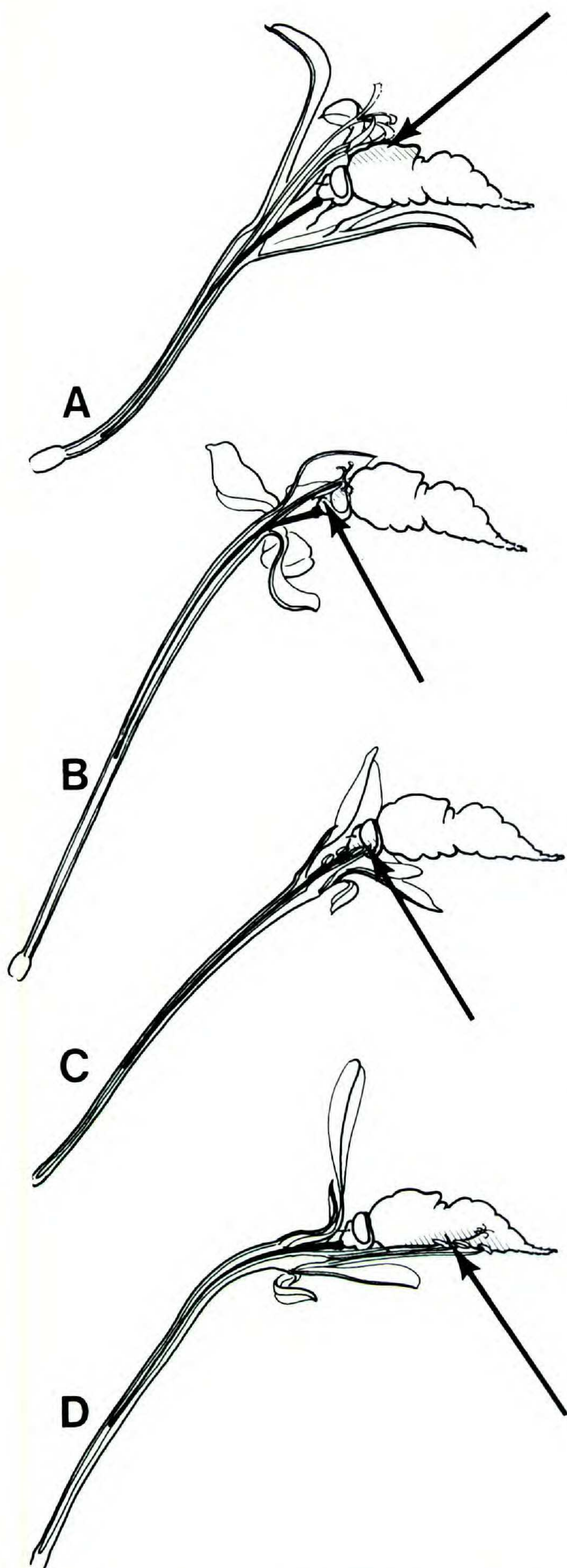


Figure 13. Differential placement of pollen on *Prosoeca peringueyi*.—A. *Babiana curviscapa*, dorsum.—B. *Lapeirousia silenoides*, frons.—C. *Pelargonium sericifolium*, face.—D. *P. incrassatum*, sternum (ventral thorax and abdomen). Hatching indicates the site of pollen deposition. (Scale: full size.)

high sugar concentration and the absence of floral odor (present in two species). The plant taxa occurring north of 29°S, i.e., in the Richtersveld and southern Namibia, comprise a distinct subset of the guild characterized by the paler-colored lilac or pale mauve flowers. This group comprises *Lapeirousia dolomitica* subsp. *dolomitica*, *Tritonia marlothii*, *Pelargonium cortusifolium*, and *P. crassicaule*.

Only *Pelargonium sericifolium* has no measurable floral nectar; we presume that it is an example of pollination by deceit (Goldblatt et al., 1995). In color and shape the flowers closely resemble those of *Lapeirousia silenoides* and *P. magenteum*. These species frequently co-occur with *P. sericifolium* and have ample amounts of nectar of relatively high sugar concentration. Two species of *Babiana* and one subspecies of *L. dolomitica* are exceptional here in having sweetly scented flowers. Presence of scent is usually considered to add to the attractiveness of the flowers, but in *Babiana* we are inclined to consider it a vestigial trait in view of its rarity among members of the guild. Most of the species of *Babiana* sect. *Babiana*, to which the *Prosoeca*-pollinated species belong, have strongly scented flowers and are bee pollinated (e.g., *B. odorata*, *B. scabrifolia*, unpublished observations).

Nectars of moderate sugar concentration and typically sucrose-rich to sucrose-dominant seem to be characteristic of plants pollinated by active insects such as bees of the family Anthophoridae and by long-tongued flies (Goldblatt et al., 1995), although not of plants pollinated by other Diptera (Baker & Baker, 1983, 1990) such as Calliphoridae, Muscidae, and Tachinidae. The nectar sugar concentrations of flowers pollinated by *Prosoeca* and other Nemestrinidae (Table 2) are typically somewhat lower than those of bee-pollinated flowers. This may be related to the difficulty of sucking up liquids of higher viscosity, as is the case in long-tongued butterflies (Johnson & Bond, 1994). The low sucrose to hexose ratios in the two species of *Pelargonium* (Table 2) contrast with the pattern in Iridaceae belonging to the guild. Species of *Pelargonium* are visited as avidly as any of the Iridaceae. Indeed, on the basis of the frequency of visits, *Pelargonium incrassatum* appears to be one of the most important nectar sources for *P. peringueyi*. This leads us to conclude that nectar sugar composition is not a significant factor in the *P. peringueyi* pollination guild.

Not all species with long perianth tubes and dark purple to crimson flowers belong to the guild. In some species that have flowers apparently conforming to the guild the lower part of the perianth tube

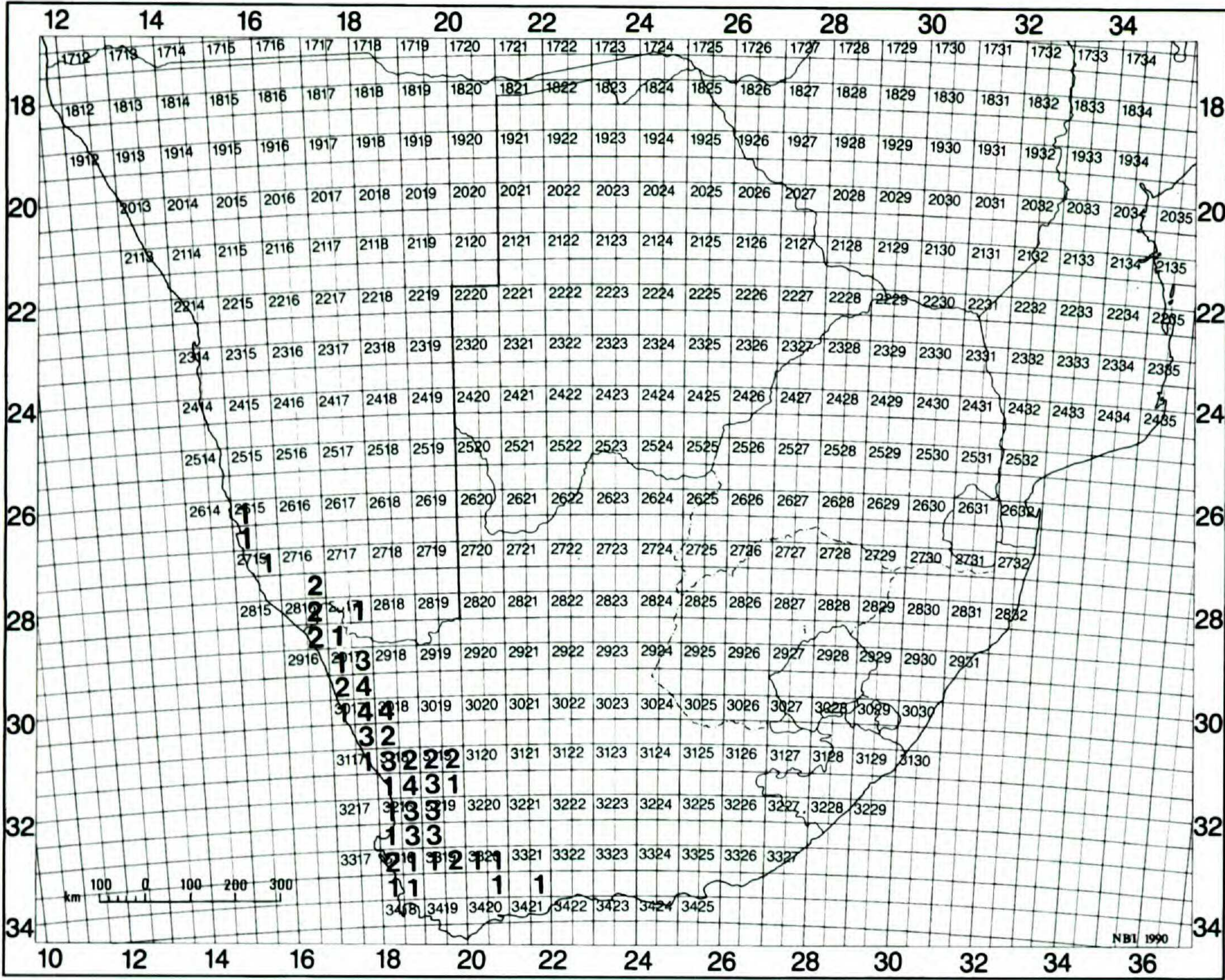


Figure 14. Map of southern Africa showing the differentiation of pollen loading sites. Figures indicate the number of different pollen-loading sites utilized by plant species per quarter-degree square of geographical latitude and longitude. The total number of species occurring in each grid is indicated in Figure 11.

is so narrow as to effectively prevent the penetration of an insect's tongue. In these cases nectar is forced into the upper part of the tube where it is accessible to a variety of insects. Long-tongued flies visiting these species may obtain nectar but will not come into contact with the pollen and stigmatic surfaces. This situation has already been described for the long-tubed species *Lapeirousia montana*, which superficially appears to be a member of a long-tongued insect pollination guild (Goldblatt et al., 1995). The tube is up to 43–55 mm long, but is so narrow in the lower half that the nectar is forced upward and lies only 10–15 mm from the mouth of the tube. The flowers are visited by a variety of bees, Lepidoptera, and bombyliid flies, all of which may accomplish pollen transfer. Likewise, we have found that whereas *B. sambucina* var. *longibracteata* and variety *unguiculata* do conform to the guild except in their scented flowers, variety *sambucina* does not. Although the perianth tubes of all three varieties are 30–55 mm long, in variety

sambucina the lower part of the tube is effectively blocked and nectar is forced into the top of the cylindrical part of the tube where it is accessible to a variety of insects. The situation in variety *sambucina* is no surprise because its distribution range is mostly outside that of *Prosoeca peringueyi* or *P. sp.* A comparable situation exists in *Babiana dregei*, which has a tube 50–65 mm long, thus longer than the mouthparts of *P. peringueyi*. In this plant, too, the tube is narrowed in the lower 20–30 mm rendering the functional tube length much shorter than the external length, and the nectar is thus available to individuals of *P. peringueyi* with tongues of moderate length.

Color of the perianth and of the nectar guides may also be misleading. *Babiana pauciflora* G. Lewis has purple flowers with tubes 35–45 mm long, but a strong fragrance, bright yellow nectar guides, and a flowering period of June appear to exclude the species from the guild. *Babiana attenuata* G. Lewis and *B. truncata* G. Lewis also have

perianth tubes in the 30–45-mm-long range, but the blue or mauve flowers have yellow nectar guides and, in the case of *B. attenuata*, fragrant flowers. We do not regard them as guild members.

THE *PROSOECA PERINGUEYI* POLLINATION GUILD

The *Prosoeca peringueyi*-*P. sp.* pollination guild (hereafter referred to simply as the *P. peringueyi* pollination guild) is unique in its combination of a long floral tube with a distinctive perianth coloring, and its restricted occurrence in so small a part of southern Africa is striking. While a long-tongued fly pollination syndrome has been described for the Cape Flora (Whitehead et al., 1987), this covered only plants with cream to pink flowers with dark nectar guides. The *P. peringueyi* guild thus deviates significantly from other long-tongued fly pollination systems. There are at least two other guilds of plant species adapted for long-tongued fly pollination in southern Africa. Late spring- and early summer-flowering species with white to cream flowers with red nectar guides (e.g., *Lapeirousia anceps* (L.f.) Ker-Gawl., *L. fabricii* (Delaroché) Ker-Gawl.) are pollinated by either *Moegistorhynchus longirostris* (Nemestrinidae), or *Philoliche gulosa*, or *P. rostrata* (Tabanidae) (Vogel, 1954; Goldblatt et al., 1995). Summer- and autumn-flowering species with long-tubed, blue, pink, or white flowers (e.g., *Nivenia stenosiphon* Goldblatt (Iridaceae, Goldblatt & Bernhardt, 1990), *Disa oreophila* H. Bol. (Orchidaceae, pers. obs.), *Gladiolus microcarpus* G. Lewis (Iridaceae, pers. obs.), and *Zaluzianskya microsiphon* (O. Kuntze) K. Schum. (Scrophulariaceae, pers. obs.)) are pollinated by *Prosoeca ganglbaueri* over a wide portion of southern Africa. Both these syndromes are quite distinct from the *Prosoeca peringueyi* pollination system in the flower color, plant and insect distribution, pollinator identity, and flowering time.

Tongue length is surprisingly variable in *Prosoeca peringueyi* and somewhat variable in *P. sp.* The variation corresponds locally to floral tube length of their nectar plants. In the Kamiesberg Mountains where *Hesperantha latifolia*, *Babiana dregei*, and *Pelargonium incrassatum* are major nectar sources and effective tube length is 20–40 mm, *P. peringueyi* has a tongue of 20–25 mm long. In other places in Namaqualand where *L. silenoides* and *B. pubescens* have floral tubes in excess of 50 mm, individuals of *P. peringueyi* have tongues 35–40 mm long. In the Olifants River Valley where *L. pyramidalis* and *L. jacquinii* are major nectar sources for *P. peringueyi* and have tubes 35–45 mm long, flies caught on these species have tongues 30–33 mm long. Clearly local variation in tube length in

the flowers of food plants is tracked by the pollinator.

The disparity between the length of floral tube in plants with the *Lapeirousia silenoides*-type flower and the shorter length of the mouthparts of the sole pollinators is quite easy to explain (Goldblatt et al., 1995). Records of nectar secretion show that these flowers secrete ample amounts of fluid for insect-pollinated flowers, and it is unlikely that dominant pollinators are ever forced to extend their mouthparts to the base of the tube unless all the nectar has been removed by earlier foragers. More importantly, Darwin (1877) hypothesized that successful pollination of spurred orchids occurred when orchids evolved floral spurs slightly longer than the tongues of their pollinators, ensuring maximum contact between the insect's head and the orchid's column by forcing the insect to ram its head down the floral throat. This has since been shown experimentally by Nilsson (1988). As in the nectariferous orchids, species with the *L. silenoides*-type flower force their pollinators to make maximum contact with the anthers and stigmatic surfaces that block or at least encircle the entrance to the floral tube.

The combined geographical ranges of all the species pollinated primarily by *Prosoeca peringueyi* and *P. sp.* (Fig. 11) are greater than the ranges so far recorded for the two fly species (Fig. 12). To the north in southern Namibia *P. peringueyi* may simply not have been collected yet. To the south, essentially below the 33rd parallel and west of the 19th north-south parallel, the guild is represented mainly by *L. jacquinii*. This species is known to be autogamous (Goldblatt et al., 1995), although it is actively pollinated by both species of *Prosoeca* within their ranges. Presumably autogamy has enabled it to extend its range outside that of its facultative pollinators. The only other species that occurs outside the ranges of the two flies is *Pelargonium magenteum*. The reasons for its wider distribution to the east of the range of *P. peringueyi* and *P. sp.* are unknown.

The potential for pollen contamination from other members of the same guild is greatly increased for plant species that share a single specialized pollinator species. One strategy to enhance segregated gene flow is differential placement of pollen on the insect body. This strategy is developed in Orchidaceae (Dressler, 1968a, b; Manning & Linder, 1992), Scrophulariaceae (Steiner & Whitehead, 1988, 1990), and various other families (Grant, 1994). In flowers of species belonging to the *P. peringueyi* pollination guild, four mutually exclusive sites have been identified. In this guild the contamination coefficient is never below 0.5, suggesting

that there is a threshold of pollination efficiency that determines the number of species that can effectively use the same landing site. In view of mechanical constraints on flower architecture in the genera involved, there appears to be a definite limit to the number of species that can enter the guild at any locality. Pollination contamination may thus be a significant factor in influencing species packing in specialist systems. Locally, the niche offered by pollination by *Prosoeca peringueyi* or *P. sp.* appears to become saturated by the presence of more than three co-flowering species. The presence of four similarly adapted species is rare.

Differential placement of pollen on an insect's body demands precise orientation of the pollinator relative to anther position. Floral zygomorphy facilitates this, and we suggest that this is an important factor in favoring genera with predominantly zygomorphic flowers.

The *Lapeirousia silenoides* pollination syndrome appears to have evolved in five different lineages in *Lapeirousia* subg. *Lapeirousia*, a taxon that includes just 21 species (Goldblatt et al., 1995). A comparably polyphyletic evolution of the syndrome appears to have occurred in *Babiana* and in *Pelargonium*, as species with this syndrome in these genera are taxonomically isolated.

ORIGIN OF THE *PROSOECA PERINGUEYI* POLLINATION GUILD

The *Prosoeca peringueyi* pollination guild involves at least six genera of plants in two families and two species of *Prosoeca* (Nemestrinidae). Although the plant species belonging to the guild and their pollinators are restricted to western southern Africa, all of the genera, both plant and insect, extend beyond the range of the guild. Other species of *Prosoeca*, both long- and short-tongued, visit flowers of various colors including white, cream, pink, lilac, blue, and yellow (Johnson, 1992; Goldblatt et al., 1995; pers. obs.). *Prosoeca peringueyi* has been observed visiting species outside the guild for nectar that are pale lilac or pink and green in color. In addition, the northern taxa of the guild are lilac or pale mauve and some have been confirmed to be pollinated by *Prosoeca peringueyi*. The original determinant for the characteristic crimson or purple color in the guild was thus apparently not directed by the innate preference of *P. peringueyi* for that particular flower color, and was in consequence presumably plant-directed.

Comparative studies of each of the guild genera suggests that pollination by long-tongued flies is apomorphic. Of the guild members only *Babiana*

has flowers in which dark blue or violet color is the plesiomorphic condition. In addition, even short-tubed species of this genus secrete fairly large amounts of nectar. Also, *Babiana* has flowers with a wide gullet, which makes access to the pollinator mouthparts easier than the narrow-tubed flowers in the other guild genera, for example, *Lapeirousia* and *Pelargonium*. These factors suggest to us that the first steps in the development of the *Prosoeca peringueyi* pollination system were through the genus *Babiana*. Significantly, both *Babiana* and *Lapeirousia*, the two genera that individually have the most species in the guild and together comprise 54% of the guild, are largely developed in arid habitats. It may be that the origin of the syndrome in *Babiana* and its subsequent development in species of *Lapeirousia* was a consequence of higher species richness in these genera in the western part of southern Africa. The predominant dark purple flower color in *Babiana* would explain the characteristic floral coloring in the *L. silenoides* pollination syndrome, unknown in other *Prosoeca* pollination guilds. Subsequently, species in other genera could be expected to enter the guild in response to the reproductive benefits derived from these pollinators.

The advantages to the plant species of a dedicated pollinator are obvious and include increased pollination success and decreased pollen contamination and loss. Pollination success in one population of *Lapeirousia pyramidalis* subsp. *regalis* that we investigated was 45% (SD \pm 25%; $n = 23$). To the pollinator, however, the energetic rewards of floral specialization are important. For large active insects that hover while foraging the energy demands are likely to be high. Long-tongued nemestrinids are capable of feeding from short-tubed flowers, but these are smaller and hold far less nectar than that typically present in the long-tubed flowers in the guild. In addition, the flies are in competition with other insects that can obtain the nectar in short-tubed flowers. Long-tubed flowers can contain large amounts of nectar that cannot be collected by short-tongued insects. They are therefore an attractive energy source for insects able to exploit it.

We speculate that there is reduced pressure to darken the flower color in the northern members of the guild. This more arid region supports both fewer plants and fewer pollinators, and a more facultatively generalist pollination system might be favored. This is borne out by the greatly extended flowering periods of *Pelargonium cortusifolium* and *P. crassicaule*, which although peaking in August and September are prolonged far beyond the flight period of *Prosoeca peringueyi*. During this time they

are presumably visited by other insects, perhaps bees and bee flies. Significantly, both species have short anthers, which will contact visitors of a range of shapes and sizes. Possibly a threshold diversity is necessary before selection pressures become strong enough to favor such specialist pollination systems.

EVOLUTIONARY IMPLICATIONS OF THE *PROSOECA* *PERINGUEYI* POLLINATION GUILD

The *Prosoeca peringueyi* pollination guild appears as distinct as other highly specific pollination systems in the African subcontinent, including those involving sunbirds, *Nectarinia* species (Rebello, 1987), oil-collecting bees in the family Melittidae (Steiner & Whitehead, 1990, 1991a), resin-collecting bees in the family Megachilidae (Steiner & Whitehead, 1991b; Armbruster & Steiner, 1992), other guilds of long-tongued flies (Goldblatt et al., 1995; Johnson & Steiner, 1995; Manning & Goldblatt, 1995), and the butterfly, *Aeropetes tulbaghia* (Johnson & Bond, 1994). Where such systems occur they contribute to the particular floral characteristics of various plant communities.

The recognition of the *Prosoeca peringueyi* pollination syndrome and the way it functions is the key to understanding the presence of a series of species with unusual dark purple or crimson flowers with long floral tubes in the flora of coastal and near interior western southern Africa. The ecological niche presented by these two flies is so specific that it will allow fly-pollinated and non-fly-pollinated members of the same genus flowering at more or less the same time to coexist with little or no hybridization. The diversity of pollination systems there is one of the reasons why some 30 species of *Babiana* (50% of the total species) and 19 species of *Lapeirousia* (48% of the total) co-occur in this area.

Like the members of the *Aeropetes tulbaghia* pollination guild (Johnson & Bond, 1994), there is strong similarity in floral morphology between members of the *Prosoeca peringueyi* guild. This suggests strong selection for floral conformity. This may be a characteristic of guilds in which the pollinator is an insect that is not flower constant.

Prosoeca peringueyi and *P. sp. nov.* may be regarded as keystone species. Such species are defined operationally as those that, by their effective disappearance from a system, would cause (directly or indirectly) the virtual disappearance of several other species. The extinction of either *P. peringueyi* or *P. sp. nov.*, but especially the former, would result in significant decreases in seed set in many of the spe-

cies in the *P. peringueyi* guild, prevent outcrossing, and might lead to their ultimate extinction.

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